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ARTICLE

Fish Community Distributions and Movements in Two Tributaries of the San Juan River, USA

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Abstract
Recognizing how stream fish communities—and their habitats—differ across space and time relative to their position in stream networks (i.e., main-stem versus tributary habitats) is increasingly important for the conservation of imperiled native fish communities in altered river networks such as those in the Colorado River basin. We studied the patterns (community composition) and processes (movements) that shape species occurrences and distributions in two tributaries of the San Juan River, Utah and New Mexico, between 2012 and 2014. Our results show that distance from the San Juan River was a strong driver of tributary fish community structure, whether through declines in species richness (Chaco Wash) or species turnover (McElmo Creek), and that these patterns coincided with habitat gradients (i.e., depth, substrate, and width). Occurrences of passive integrated transponder (PIT)–tagged fish at a stationary antenna in McElmo Creek just upstream of its confluence with the San Juan River varied by species but generally were associated with spring spawning migrations (Flannelmouth Sucker *Catostomus latipinnis*, Razorback Sucker *Xyrauchen texanus*), exploratory movements (Colorado Pikeminnow *Ptychocheilus lucius*), and monsoon flooding (Channel Catfish *Ictalurus punctatus*, Razorback Sucker). Occurrences of PIT-tagged fish in Chaco Wash were dominated by endangered Razorback Suckers and Colorado Pikeminnows, suggesting that this habitat supplies useful habitat, forage, or both. Given the common occurrences of native fishes in these tributaries, incorporating these habitats into basinwide management actions seems necessary to fully understand the spatiotemporal dynamics of native and nonnative fish communities.

Recent studies have reported occurrences of "big-river" endangered species in smaller tributary systems in the American Southwest, sparking an interest in the role of these habitats in stream networks (Wick et al. 1991; Bottcher et al. 2013; Fresques et al. 2013). Tributary habitat use by fishes is dependent on the degree of permanence of water in the tributary (ephemeral or perennial), the size of the tributary, and distance from the main-stem river (Osborne and Wiley 1992; Datry et al. 2014); moreover, these habitats can support critical life history stages of fishes (Schlosser 1991; Fausch et al. 2002). Documenting the occurrences and movements of species of conservation concern as well as other native and nonnative fishes in these tributaries will help inform management efforts to preserve critical habitats and ensure the persistence of these imperiled species.

The Colorado River basin is a highly modified stream network that supports relict populations of endemic fishes in the midst of massive water development projects, habitat alteration, and species introductions (Minckley and Deacon 1968; Poff et al. 1997). Alterations exist throughout the major subbasins in the upper Colorado River basin: the San Juan, Duchesne, Yampa, Green, Gunnison, and White rivers (Bottcher et al. 2013; Webber et al. 2013). Despite widespread alterations, the stream networks within these subbasins continue to

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be regarded as key native fish habitats, serving to maintain migratory routes (Irving and Modde 2000), meet life stage–specific needs (i.e., spawning, refuge, and feeding; Childs et al. 1998; Robinson et al. 1998; Weiss et al. 1998), and allow for population conservation (Bestgen et al. 2007). However, small tributary systems are infrequently included in management actions, probably because of their size, remoteness, straddling of political boundaries, and unknown contributions to endangered species or adjacent critical habitats (Clarkson et al. 2012; Pool et al. 2013).

While relatively few resources have been spent exploring small tributaries, evidence of sensitive and endangered native fishes' use of these habitats is growing (Bezzerides and Bestgen 2002; Finney 2006; Compton et al. 2008). For example, a passive integrated transponder (PIT)-tagging study identified movements of endangered Bonytail *Gila elegans*, Colorado Pikeminnow *Ptychocheilus lucius*, and Razorback Sucker *Xyrauchen texanus* in the San Rafael River, Utah, a small tributary to the Green River (Bottcher et al. 2013). Additionally, sensitive native species, including Flannelmouth Sucker *Catostomus latipinnis*, Bluehead Sucker *C. discobolus*, and Roundtail Chub *G. robusta* occur in habitats ranging from main-stem rivers to small tributaries, and declines of these species are becoming a conservation concern within the Colorado River basin (Compton et al. 2008; Dauwalter et al. 2011; Walsworth et al. 2013). Tributaries that support native fish may also be important components of nonnative fish dynamics, which could ultimately diminish the conservation potential of native fishes through hybridization (McDonald et al. 2008; Quist et al. 2009), competition (Walsworth et al. 2013), or predation (Marsh and Brooks 1989; Brandenburg and Gido 1999; Webber et al. 2012).

Even though several studies have explored fish community dynamics in the San Juan River (i.e., Gido et al. 1997; Propst and Gido 2004; Franssen and Durst 2013), explicit consideration of fish distributions in tributary habitats has been limited to an unpublished data review (Miller and Rees 2000) and the mention of spawning movements by Colorado Pikeminnows around the confluence of the Mancos River (Ryden and Ahlm 1996). On the basis of the limited data available for many tributaries prior to 1970, Miller and Rees (2000) suggested that the composition of tributaries has changed from native fish communities to blended communities of native and nonnative species associated with flow and habitat alterations. Fresques et al. (2013) provided the first published record of endangered Colorado Pikeminnows in McElmo Creek, a small tributary of the San Juan River, but other species' use of the tributary networks relative to the main-stem San Juan River remains poorly documented. The overarching objective of this study was to document occupancy and movements within two small, but mainly perennial, tributaries of the San Juan River by a fish community comprising intensively managed populations of endangered Colorado Pikeminnows and Razorback Suckers; native Flannelmouth Suckers, Bluehead Suckers, and Roundtail Chub; and several nonnative fishes. We combined systematic sampling of two tributaries over spatial and temporal gradients with a PIT-tagging study to quantify the seasonal distributions, catch, and movements of the fishes as well as stream geomorphology.

Dispersal and habitat limitations have been implicated in the patterns of fish community composition and species abundance throughout stream and reservoir networks (i.e., proximity to confluences or different habitats; Osborne and Wiley 1992; Falke and Gido 2006; Thornbrugh and Gido 2010). Thus, we hypothesized that distance from the main-stem San Juan River would best explain community structure, i.e., that species more indicative of main-stem communities would blend with tributary communities near the San Juan River and that communities distant from the main stem would consist of tributary-associated species. Further, we hypothesized that the habitats would display gradients of decreasing width and depth with distance from the San Juan River. We also hypothesized that species would differ in the annual timing and frequency of their movement into and within these tributaries related to spawning migrations and other critical processes related to season and environmental conditions associated with spring runoff and summer monsoons.

METHODS

Study area.—The San Juan River is a main tributary to the Colorado River and drains 99,200 km^2 from its headwaters in southwest Colorado through New Mexico, Arizona, and Utah before entering Lake Powell 365 km downstream of Navajo Dam (Franssen and Durst 2013). Navajo Dam impounded the San Juan River in 1962, inundating 56 km of the river and partly modifying the flow and temperature regimes for 288 km downstream before entering Lake Powell (Ryden and Ahlm 1996; Franssen and Durst 2013). The Animas River is the largest tributary to the San Juan River; it drains 2,823 km^2, lacks a major main-stem impoundment, and enters the San Juan River at Farmington, New Mexico. Critical habitat for federally listed endangered species is located between the Hogback Diversion near Farmington (rkm 256) and Lake Powell (rkm 0), although endangered fish have been found—and stocked—upstream of that boundary.

Two small tributaries entering the San Juan River within designated critical habitat have been insufficiently studied but might provide habitat for native and nonnative fishes: McElmo Creek and Chaco Wash (Figure 1). McElmo Creek drains 1,818 km^2 in Colorado and Utah before joining the San Juan River 163 km upstream of Lake Powell (Navajo Nation Environmental Protection Agency 2012). McElmo Creek has one perennial tributary, Yellow Jacket Creek, which enters it near the Colorado–Utah border, approximately 32 km upstream of the San Juan River. McElmo Creek was historically an intermittent stream, but irrigation and water development stemming from the creation of McPhee Reservoir in 1986

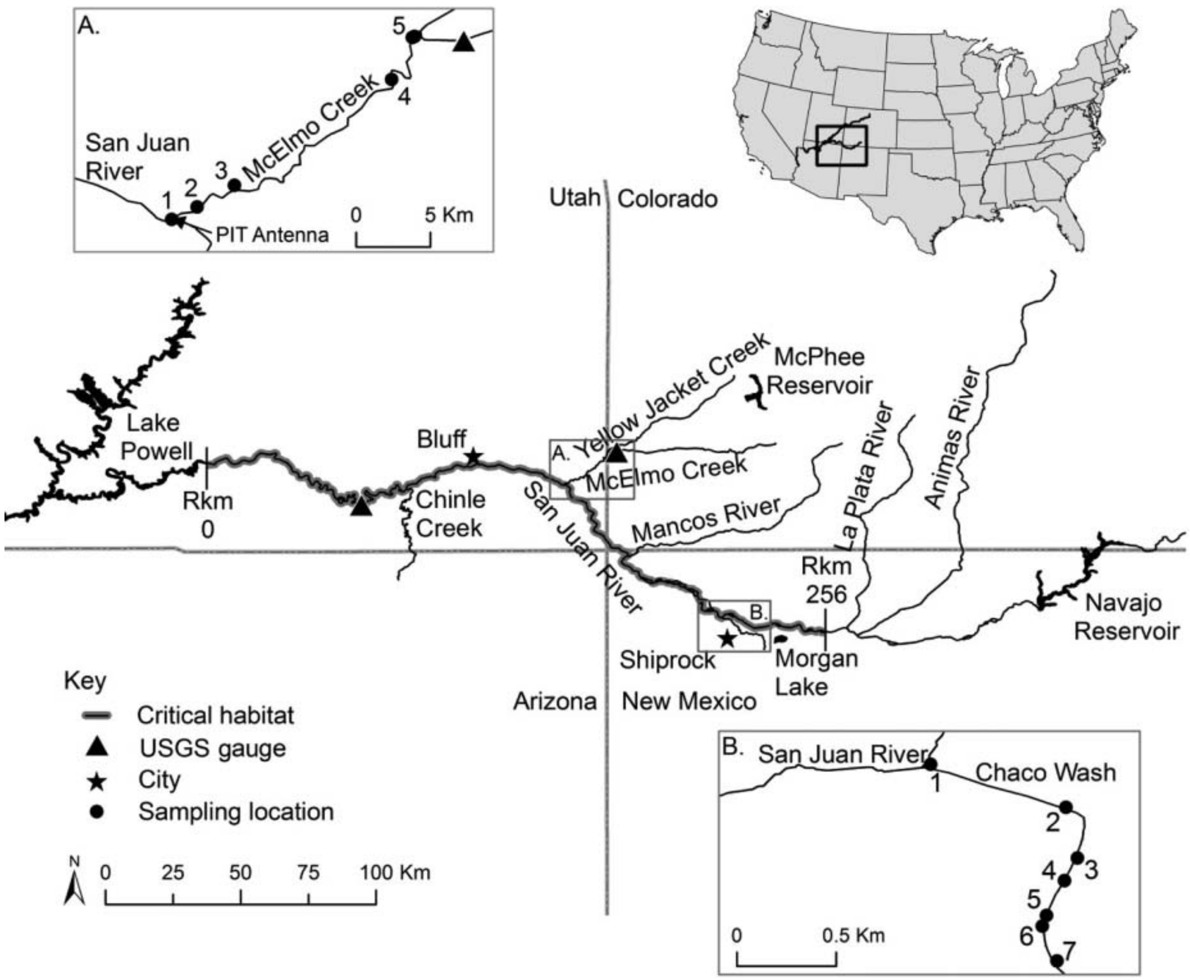

FIGURE 1. Map of the San Juan River basin, showing tributary sites in the inset maps, relevant cities, U.S. Geological Survey stream gauges, and designated critical habitat.

effectively transformed it to a perennial system by capturing water from the Dolores River basin (Fresques et al. 2013). Riparian vegetation is dominated by Russian olive *Elaeagnus angustifolia* but also includes saltcedar *Tamarisk* spp., willow *Salix* spp., and rarely, eastern cottonwood *Populus deltoides*. Land use practices include agriculture, oil and natural gas development, and grazing. Chaco Wash drains an area of 11,396 km^2 to the confluence of the San Juan River east of Shiprock, New Mexico, 243.5 km upstream from Lake Powell (Figure 1). Despite its large drainage area, Chaco Wash has perennial flow only downstream of the outlet from Morgan Lake, 6 km upstream of the confluence with the San Juan River. Morgan Lake was created in 1961 and is the site of a coal-burning power plant that diverts San Juan River water for a reservoir used to cool the generators. Flows in summer 2012 maintained connectivity throughout the year; in 2013, however, flows were disconnected upstream of the study reach. Riparian vegetation is similar to that of McElmo Creek, and land use along Chaco Wash is primarily sheep and cattle grazing.

Fish sampling.—To characterize the spatial and seasonal variation in fish communities along a longitudinal gradient away from the San Juan River, five sites in McElmo Creek (Figure 1) were sampled three times in summer (June 2012, May 2013, and June 2014), twice in fall (October 2012 and November 2013), and twice in spring (March 2013 and 2014). All sampling dates occurred when McElmo Creek discharge was near base-flow amounts with good visibility (mean daily discharge < 0.57 m^3/s). At each site, single-pass backpack electrofishing with two netters was used to sample fixed-distance reaches of 300 m. At site 1 we performed three 10–20-m seine hauls using a bag seine (6.1×1.22 m, 1.69-mm mesh) in addition to electrofishing to effectively capture small-bodied fishes in the large, wide (~12-m) glide habitat. All fish were identified, measured, and released.

In Chaco Wash, the confluence with the San Juan River and six consecutive pool habitats upstream were sampled five times in summer (June 2012 and 2013, July 2012, and August 2012 and 2013), twice in fall (October 2012 and November 2013), and twice in spring (March 2013 and 2014). Three seine hauls using the bag seine were conducted at the mouth of Chaco Wash because the greater depths and higher flow at the confluence with the San Juan River prevented electrofishing. In pools upstream of the confluence, extremely high turbidity and conductivity reduced electrofishing efficiency, while coarse substrates or very thick silt (>30 cm) reduced seining efficiency. Thus, we combined the methods and chased fish with a backpack electrofisher downstream through the riffle and into the pool where a bag seine was positioned across the width of the stream. Pool sizes varied considerably (from 20.7 m to >400 m long), and since our sampling efficiency was compromised by silt or depth, we standardized sampling lengths to the length of the smallest pool habitat (20.7 m). Because of the extreme differences in tributary size, habitats, and sampling events between McElmo Creek and Chaco Wash, qualitative comparisons (e.g., catch rates) were difficult to interpret.

*Habitat sampling.—*Spatial variation in habitat was estimated by measuring wetted width at 10 equally spaced transects along the length of each site; depth and substrate, the latter using a modified Wentworth scale (0 = silt [<0.3 mm], 1 = sand [0.3–2 mm], 2 = gravel [2–64 mm], 3 = cobble [64–250 mm], 4 = boulder [>250 mm], and 5 = bedrock; Bovee and Milhous 1978), were also measured 10 times along each transect. Habitat measurements were taken concurrently with fish sampling at McElmo Creek. The distance of sites from the San Juan River was based on high-resolution National Hydrography Dataset data (1:24,000/1:12,000 scale) using ArcGIS version 10.0 mapping software. Discharges from McElmo Creek and the San Juan River were collected to identify a potential environmental trigger for fish movements. Daily discharge was recorded by U.S. Geological Survey streamflow stations in McElmo Creek and from the San Juan River near Bluff, Utah (Figure 1). Discharge was not recorded at Chaco Wash. Chaco Wash habitat variables were measured using the same methods as at McElmo Creek except that measurements were made only along two transects per pool due to the much smaller area sampled. Habitat measurements at Chaco Wash were made in June and October of 2012 and March and June 2013.

*Movement study.—*To identify the movements of fish at tributary mouths, we implanted all large-bodied fishes (defined as fishes with an adult total length >230 mm) that were greater than 115 mm—besides White Sucker *Catostomus commersonii* and White Sucker hybrids—with a 12-mm, 134.2-kHz, full-duplex PIT tag. Opportunistic tagging of fish outside of our fixed sample sites was done throughout McElmo and Yellow Jacket creeks as well as in several reaches of the San Juan River between May 2012 and March 2014. Additionally, stocked Colorado Pikeminnows and Razorback Suckers in the main stem had been PIT-tagged by state (Utah Division of Wildlife Resources and New Mexico Department of Game and Fish) and federal (U.S. Fish and Wildlife Service) agencies during river monitoring trips or prior to stocking events that began in the mid-1990s. Other native fishes in the McElmo Creek basin upstream of our study sites were PIT-tagged by Colorado Parks and Wildlife prior to and during the study period.

To evaluate the movement of fishes into and out of McElmo Creek, we installed a PIT tag antenna array that spanned the width of the creek on May 2, 2012, approximately 150 m upstream from the confluence with the San Juan River. This five-antenna array had a pass-over design, where antennas were anchored flat to the streambed (i.e., underwater) and fish were assumed to track the streambed as they moved. Detection ranges, which were tested occasionally throughout the study period, ranged from 10 to 51 cm. Detection data for this study ended July 31, 2014. Some, but not all, antennas were disabled during disturbance events in January (ice flows) and October 2013 (monsoonal flooding). For this reason, directional data are not presented here.

We deployed a portable PIT antenna (3.05 × 0.76 m) in Chaco Wash 27 m upstream from the confluence with the San Juan River from June 6 to July 17, 2013. This antenna was installed with a pass-through design, where one long side of the rectangular antenna was anchored to the streambed in mid-channel perpendicular to the bank and then positioned upright to detect movements through a cross section of the water column. Additionally, we installed block nets between the streambank and the sides of the antenna to direct fish through the antenna. Detection ranges were tested during weekly battery changes and varied from 13 to 46 cm. This antenna was destroyed by flooding during the beginning of the monsoon season on July 17, 2013.

*Data analysis.—*We used analysis of variance (ANOVA) to investigate habitat variables, species richness, and species distributions across sites at each tributary. If the ANOVA showed a significant difference among sites ($P < 0.05$), we used Tukey's honestly significantly different (HSD) test to evaluate which particular sites differed from each other. Spatiotemporal variation in the fish community structure of McElmo Creek and Chaco Wash was characterized with canonical correspondence analysis (CCA; vegan package version 2.0-10 in R version 3.0.3; R Development Core Team 2008). Species count data were objects or dependent variables. To reduce the influence of extreme catches, values were $\log_{10}(x + 1)$ transformed. In McElmo Creek, data for rare species (i.e., species sampled at two or fewer sites throughout the study) and samples with low catch (<12 total fish in a sample) were removed due to their undue influence on the analysis and its subsequent interpretation. In Chaco Wash, species that made up less than 2% of the total sample were considered rare and omitted from the analysis. Habitat variables included distance upstream from the confluence with the San Juan River, wetted width, mean depth, maximum depth, substrate scores, and season (fall, spring, or summer); based on visual inspection of the distributions of their values, these data were not transformed. Multicollinearity was assessed for all environmental variables via variance inflation factors (VIFs), and redundant variables were removed if VIFs were >10. The significance of CCA axes and habitat variables was analyzed with permuted ANOVA.

RESULTS

Habitat

All habitat variables differed significantly across sites in each tributary and warranted post hoc analysis with Tukey's HSD (Figure 2). For both streams, wetted widths were significantly greater at the site nearest to the San Juan River and decreased with distance from the main stem. The mean depth at Chaco Wash was significantly different between sites, but post hoc comparisons revealed that only the sixth site was significantly shallower than the first site. Mean and maximum depths increased moving upstream in McElmo Creek, the most upstream site being significantly deeper than the first two sites nearest to the San Juan River. Substrate sizes were significantly larger in upstream reaches in Chaco Wash, transitioning from fine substrates dominated by silt and sand nearest the San Juan River to bedrock stream bottoms at upstream sites. Substrates in McElmo Creek were significantly larger in upstream reaches, but mean substrate size was between 1 (sand) and 2 (gravel), indicating that substrate was more consistently sized and mixed in McElmo Creek.

The San Juan River has much greater flow than McElmo Creek, with some synchronization in discharge between the two systems (Figure 3). Flow spikes were associated with the monsoon season in 2012 and 2013 in both the San Juan River and McElmo Creek, but spring releases simulating runoff from snowmelt were present in May and June only in the San Juan River while concurrent flows in McElmo Creek were constantly low. The flow spike at McElmo Creek in late May 2014 is attributable to a brief rainstorm, not a prolonged melting or runoff event.

Fish Sampling

McElmo Creek had a fish community of 16 species and 3 hybrid suckers (Table 1). Chaco Wash contained 13 species and 1 hybrid sucker (Table 2). Species that were found only in McElmo Creek included Roundtail Chub, Bluegill, and White Sucker. One Razorback Sucker was collected from each tributary at the sites closest to the San Juan River. In November 2013 at Chaco Wash, 112 small Colorado Pikeminnows (<90 mm total length) were collected; however, since this was immediately after annual stocking of age-0 fish, only the 10 fish greater than 90 mm were retained for further analysis. Two sites in Chaco Wash produced fishless samples (site 3 in July 2012 and site 5 in June 2013).

Mean species richness in McElmo Creek and Chaco Wash was highest at sites closest to the San Juan River (Figure 4). An ANOVA testing for differences in species richness among sites in McElmo Creek was significant, but post hoc tests with Tukey's HSD indicated a significant difference only between site 1 and site 4 ($P = 0.02$). An ANOVA testing for differences among sites in Chaco Wash was highly significant, sites 1 and 2 (nearest the confluence) having significantly higher richness (~5 species/site) than upstream sites 3–7 (~2 species/site), based on Tukey's HSD.

Flannelmouth Suckers and Speckled Dace had consistently high catches throughout McElmo Creek that did not differ significantly among sites (Figure 5). Roundtail Chub and Bluehead Suckers had increasing catches with distance from the San Juan River, but only the Roundtail Chub catch was significantly greater; post hoc tests with Tukey's HSD found that the most upstream site had the highest catch. Catches of Colorado Pikeminnows were relatively low throughout McElmo Creek and did not differ significantly among sites. Nonnative Channel Catfish, Black Bullheads, and Red Shiners all had patterns of relatively low catches that did not differ significantly among sites.

Native Flannelmouth Suckers, Speckled Dace, and Colorado Pikeminnows had constant catches throughout Chaco Wash and did not significantly differ among sites (Figure 6). Nonnative Channel Catfish and Black Bullheads did not significantly differ in catch relative to distance from the San Juan River. The Red Shiner catch differed significantly among sites, but post hoc analysis did not find any significant differences between pairs of sites.

Fish–Habitat Associations

Canonical correspondence analysis illustrated the associations between fish community structure and the environmental variables measured. For McElmo Creek, no habitat variables had VIFs >10; thus, all were included in the analysis. Permuted ANOVA of the McElmo Creek habitat variables found that distance from the San Juan River, mean wetted width, and season were significantly associated with fish community structure ($P < 0.005$). The first three CCA axes were significant, the first two being highly significant ($P < 0.005$). The variation among sites along CCA axis 1 (which explained 43.6% of the variance) indicated that the McElmo Creek fish community transitioned from a blended native and nonnative community nearest to the San Juan River to a native fish–dominated community in the upstream sites, largely influenced by Roundtail Chub and Bluehead Suckers (Figure 7). The second axis (which explained 22.3% of the variance) generally accounted for the temporal variation in fish communities and habitat variables. Channel Catfish had negative axis 2 scores and were associated with samples in fall. Generally, fall sampling dates in McElmo Creek were negatively loaded on the second axis because of greater depths after the monsoon season. Flannelmouth Suckers and Red Shiners had similar temporal associations to spring and early summer samples as well as broad spatial distributions. Speckled Dace were more associated with summer and fall samples and were negatively loaded on the second axis due to their rarity in spring samples, in contrast to the patterns seen in Flannelmouth Suckers and Red Shiners. The third axis ($P < 0.05$) was driven by higher proportions of relatively rare species (e.g., Fathead Minnow and Largemouth Bass) in samples with relatively low total catch (<30 total fish) but had no apparent spatial or temporal trend when plotted and was not shown.

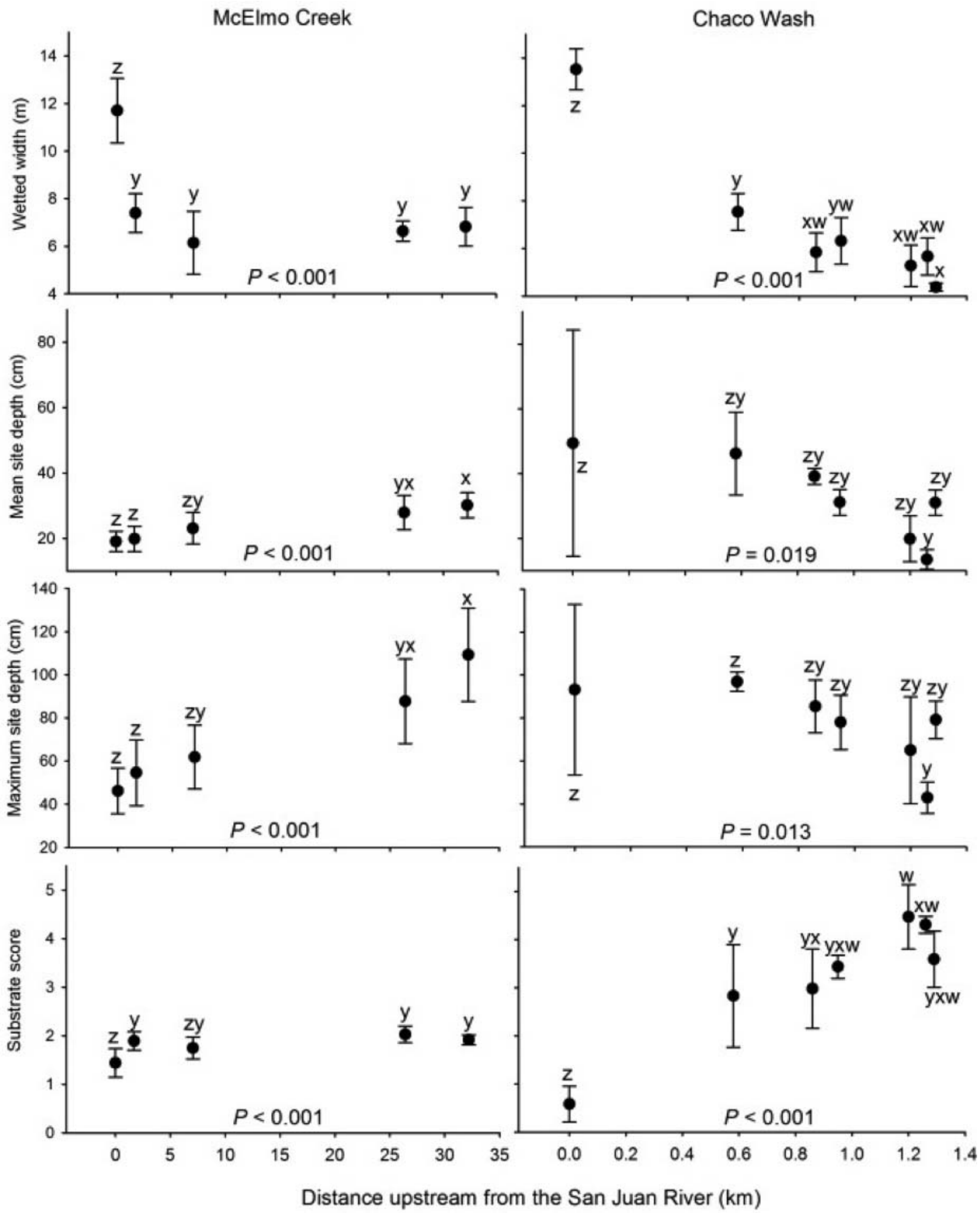

FIGURE 2. Mean wetted width, mean depth, maximum depth, and modified Wentworth substrate scores relative to distance from the confluence with the San Juan River in McElmo Creek (data recorded in May and October 2012; March, June, and November 2013; and March and June 2014) and seven seasonally sampled habitats in Chaco Wash (June and October 2012 and March and June 2013). Error bars = 95% confidence intervals; means with different lowercase letters are significantly different ($P < 0.05$).

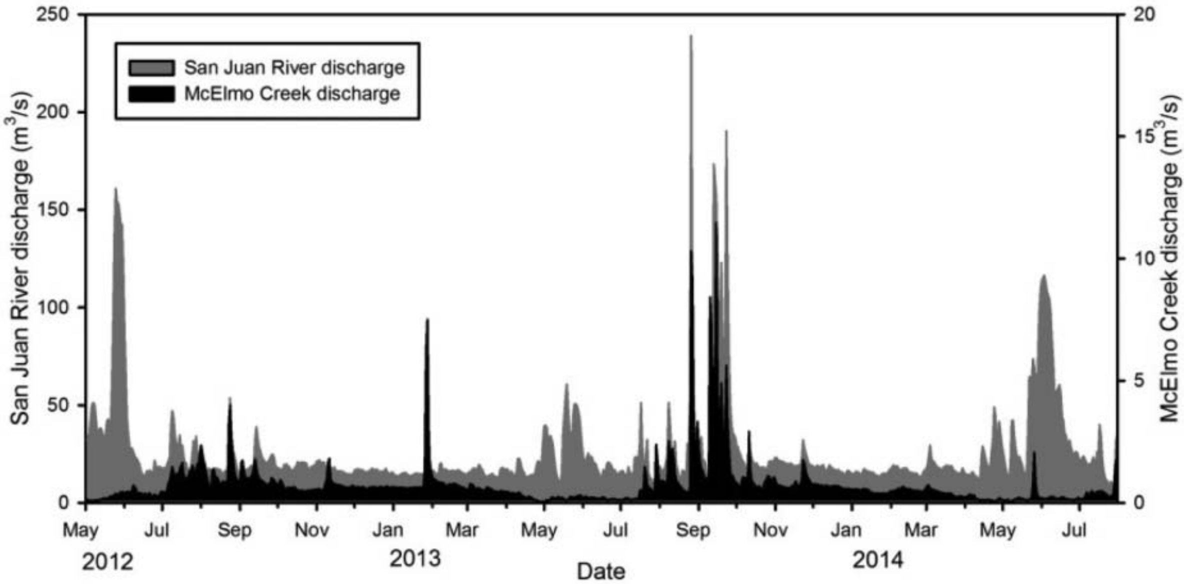

FIGURE 3. Comparison of San Juan River (USGS gauge 9379500, Bluff, Utah) and McElmo Creek (USGS gauge 9372000, Colorado–Utah border) discharge between May 2, 2012, and July 31, 2014.

TABLE 1. Numbers of fish of various species sampled at five sites in McElmo Creek upstream of its confluence with the San Juan River in 2012 (June and October), 2013 (March, May, and November), and 2014 (March and June). Asterisks denote nonnative species or hybrids that include nonnative species.

	Site number (distance from San Juan River [km])					
Species	1 (0.3)	2 (1.9)	3 (7.05)	4 (26.4)	5 (32.2)	Total
Flannelmouth Sucker	299	305	210	265	453	1,532
Speckled Dace *Rhinichthys osculus*	31	41	58	53	66	249
*Red Shiner *Cyprinella lutrensis*	105	25	14	2	20	166
*Channel Catfish *Ictalurus punctatus*	35	16	63	2	20	136
Bluehead Sucker	2	6	1	23	47	79
Roundtail Chub	1	0	0	2	58	61
Colorado Pikeminnow	24	2	1	1	3	31
*Black Bullhead *Ameiurus melas*	14	8	7	0	1	30
*Fathead Minnow *Pimephales promelas*	17	2	0	0	0	19
*Largemouth Bass *Micropterus salmoides*	6	0	0	0	0	7
*Green Sunfish *Lepomis cyanellus*	0	0	0	0	4	4
Hybrid sucker[a]	0	0	0	0	3	3
*Hybrid sucker[b]	0	0	0	0	3	3
*Western Mosquitofish *Gambusia affinis*	2	0	0	0	0	2
*White Sucker	0	0	0	0	2	2
*Hybrid sucker[c]	0	0	0	1	0	1
*Bluegill *Lepomis macrochirus*	1	0	0	0	0	1
Razorback Sucker	1	0	0	0	0	1
*Common Carp *Cyprinus carpio*	0	1	0	0	0	1
Total	538	407	354	349	680	2,328

[a]Flannelmouth Sucker × Bluehead Sucker.
[b]White Sucker × Flannelmouth Sucker.
[c]White Sucker × Bluehead Sucker.

TABLE 2. Numbers of fish of various species sampled on nine dates at seven sites in Chaco Wash upstream of its confluence with the San Juan River during 2012 (June, July, August, and October), 2013 (March, June, August, and November), and 2014 (March). Asterisks denote nonnative species or hybrids that include nonnative species.

Species	Site number (distance from the San Juan River [m])							Total
	1 (0)	2 (570)	3 (867)	4 (939)	5 (1,161)	6 (1,219)	7 (1,246)	
Speckled Dace	110	23	10	9	6	11	14	183
Flannelmouth Sucker	81	29	7	19	12	1	7	156
*Black Bullhead	6	12	23	24	33	22	24	144
*Red Shiner	47	29	7	0	2	1	0	86
Colorado Pikeminnow	35	15	8	3	6	4	3	74
*Channel Catfish	16	34	11	3	1	0	5	70
Bluehead Sucker	8	10	3	10	3	3	1	38
*Common Carp	12	2	0	0	1	0	0	15
*Fathead Minnow	11	1	0	0	0	0	0	12
*Western Mosquitofish	4	3	0	0	2	0	0	9
*Largemouth Bass	1	5	0	0	1	0	0	7
*Green Sunfish	0	2	0	0	0	0	1	3
Razorback Sucker	1	0	0	0	0	0	0	1
*Hybrid sucker[a]	0	0	0	1	0	0	0	1
Total	332	165	69	69	67	42	55	799

[a]White Sucker × Bluehead Sucker.

Chaco Wash had two variables (mean wetted width and mean depth) with VIFs >10, which thus were excluded from the analysis. The Chaco Wash sites exhibited some temporal variation in fish community structure that was more associated with spatial proximity to the San Juan River. The first CCA axis was marginally significant based on a permuted ANOVA of axis scores ($P < 0.1$) and explained 57.7% of the variance. This axis generally showed a pattern of spatial variation in stream fish community distribution, weakly associated with distance from the main stem. The second axis explained only 28.2% of the variance in fish community structure and was not significant ($P = 0.29$). Only Channel Catfish catch was associated with maximum depth, and Black Bullheads were associated with distance from the San Juan River (Figure 8). Catches of Speckled Dace, Red Shiners, and Flannelmouth Suckers were greatest near the confluence. However, Flannelmouth Suckers and Red Shiners were more associated with the confluence habitat or the first pool, in contrast to the greater upstream distributions of Speckled Dace and Black Bullheads, which generated a negative second-axis score Colorado Pikeminnows and Bluehead Suckers had similar positions along an intermediate gradient between depth and distance from the San Juan River.

Fish Movements

Between June 2012 and July 31, 2014, we tagged 5,486 fish consisting of 11 species and 1 native hybrid sucker in McElmo Creek, Chaco Wash, and the San Juan River (Table 3). We detected a total of 2,466 fish representing 9 species and the hybrid sucker at the McElmo Creek PIT antenna array, with Flannelmouth Suckers, Channel Catfish, Razorback Suckers, and Colorado Pikeminnows accounting for over 98% of the fish detected (Table 3). Flannelmouth Suckers were detected in very high abundance (hundreds of individuals) in spring 2013 and 2014 (Figure 9). Channel Catfish were detected both years, with peak abundance of more than 100 individuals occurring in early summer through fall. The lack of Flannelmouth Sucker and Channel Catfish detections in spring 2012 is attributable to the fact that no individuals of those species had been tagged at that point; as it happened, a large number of tagged Razorback Suckers and Colorado Pikeminnows from other research projects were detected. Razorback Suckers were detected during spring (especially in May, when over 40 individuals were detected each year) and in fall 2012 (November especially). Colorado Pikeminnows were detected in relatively low numbers (<10 individuals per month) throughout the year, but abundances were highest from late summer through December in both years. At Chaco Wash in summer 2013, using the portable PIT antenna, we detected a total of 135 fish representing six species; Razorback Suckers and Colorado Pikeminnows accounted for over 89% of the detections (Table 3).

DISCUSSION

The data presented above support our hypotheses that communities and habitat would be associated with distance from

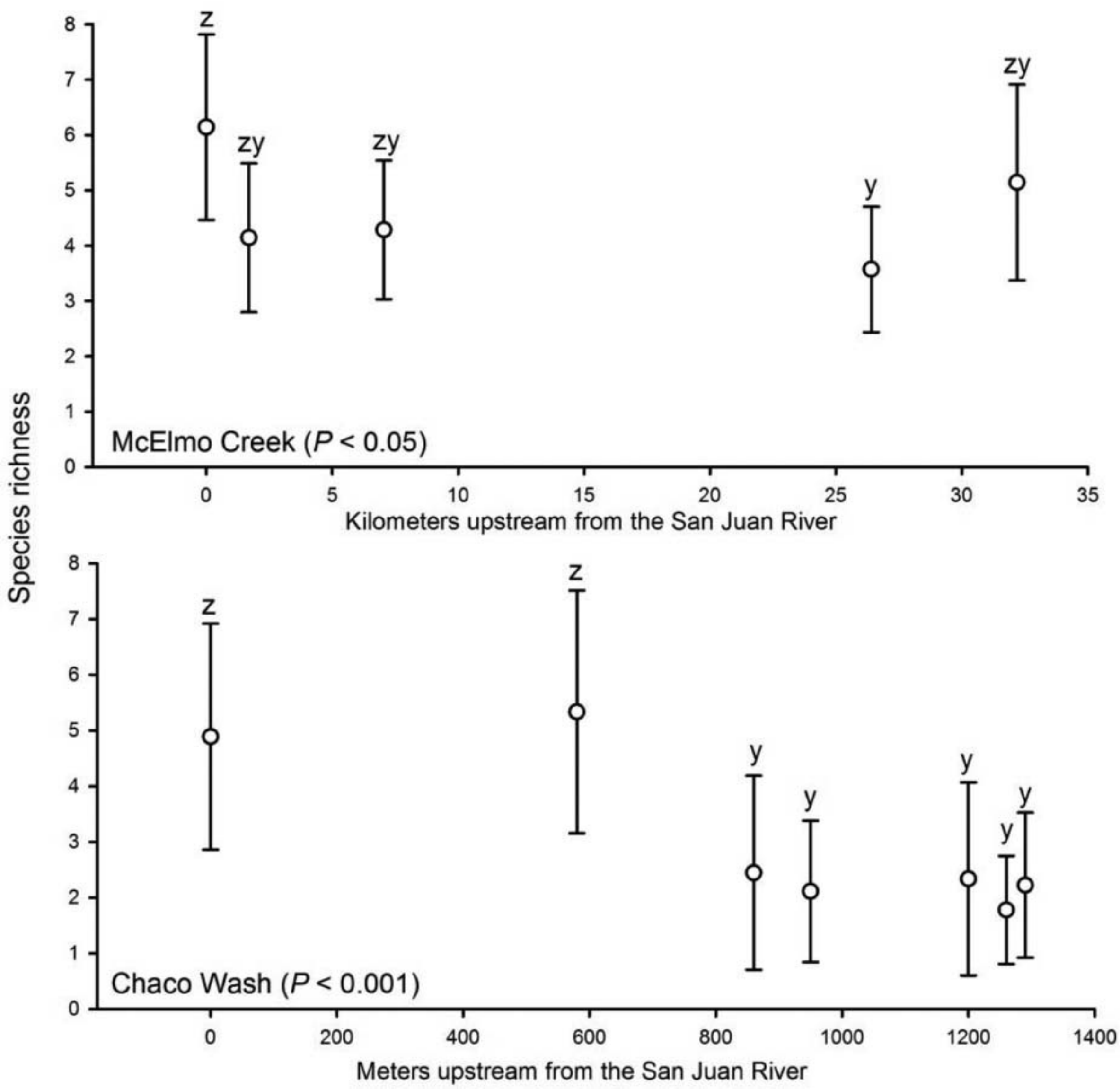

FIGURE 4. Species richness in Chaco Wash and McElmo Creek, as determined by seasonal sampling from 2012 through 2014. Sites with different lowercase letters were statistically different (ANOVA: $P < 0.05$).

the main-stem San Juan River. The fish communities in McElmo Creek and Chaco Wash included six and five native species, respectively, but the spatial dynamics—and our sampling methods—differed between the two systems, which limits comparisons. Chaco Wash is a linearly structured stream with diminishing habitat (i.e., water) and species richness upstream, whereas McElmo Creek is a branching network with an upstream tributary (Yellow Jacket Creek) that resulted in more species turnover in moving upstream from the San Juan River. The confluences with the San Juan River structured fish communities at both McElmo Creek and Chaco Wash, but the greater area and more perennial flow of McElmo Creek at its confluence with Yellow Jacket Creek probably provided a habitat complex that maintained higher diversity and abundance farther (i.e., >30 km) from the main-stem river.

The patterns of increased diversity and catches of certain species at McElmo Creek sites adjacent to confluences (sites 1 and 5) highlight potentially important habitat in these areas. For example, more headwater species such as Roundtail Chub and Bluehead Suckers were caught nearest to Yellow Jacket Creek, whereas Razorback Suckers, a big-river specialist, were found at the San Juan River confluence in both McElmo Creek and Chaco Wash. Nonnative fish abundance at confluence zones differed among seasons and streams. Red Shiner abundance was greatest at the confluence zones of McElmo Creek and Chaco Wash and was higher than any other

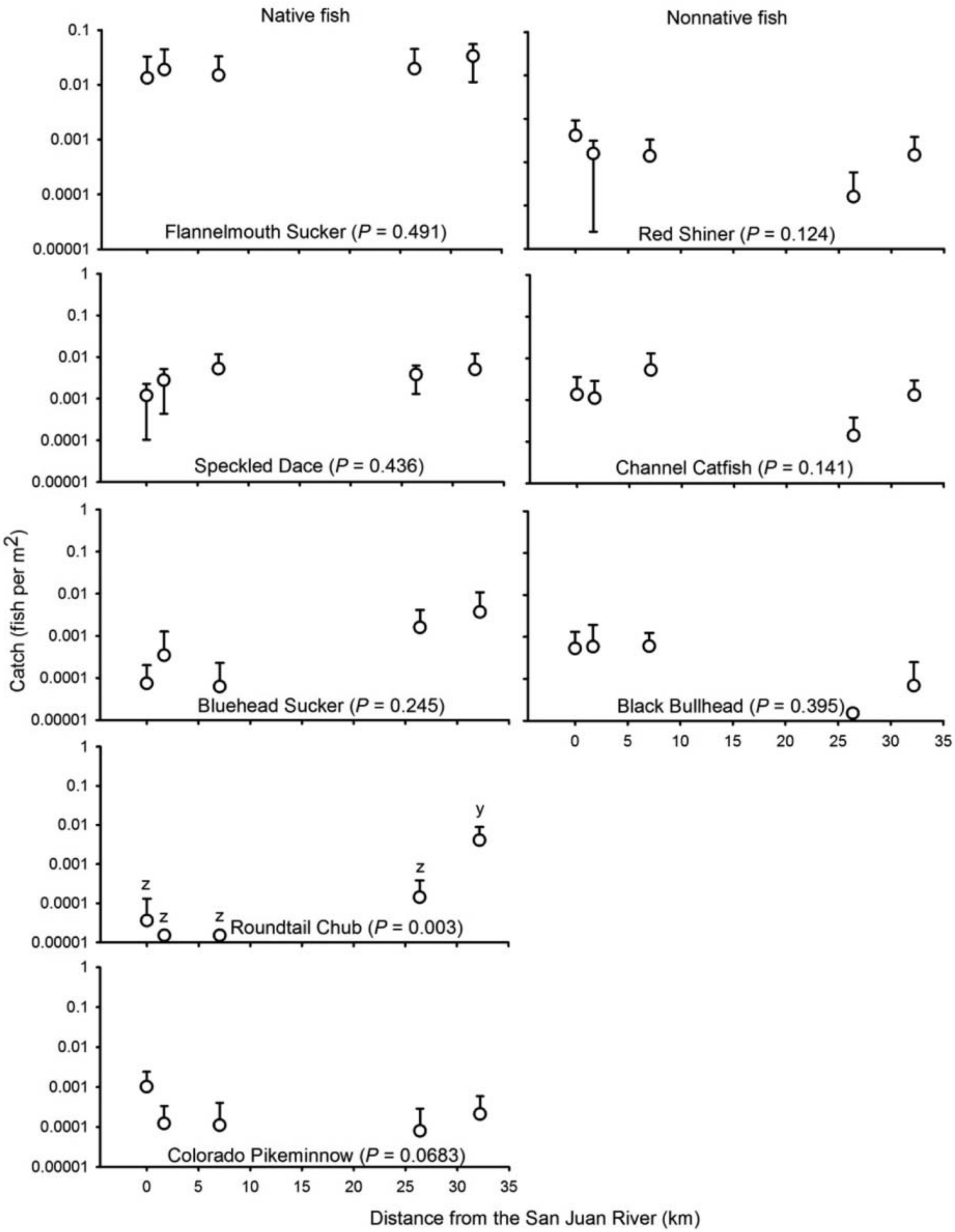

FIGURE 5. Catches of eight frequently encountered species sampled in McElmo Creek at sites distributed upstream from the confluence with the San Juan River in 2012 (June and October), 2013 (March, May, and November), and 2014 (March and June). The error bars = 95% CIs; the *P*-values indicate the probabilities of the catches of the observed species differing by chance and were tested at the 0.05 level of significance.

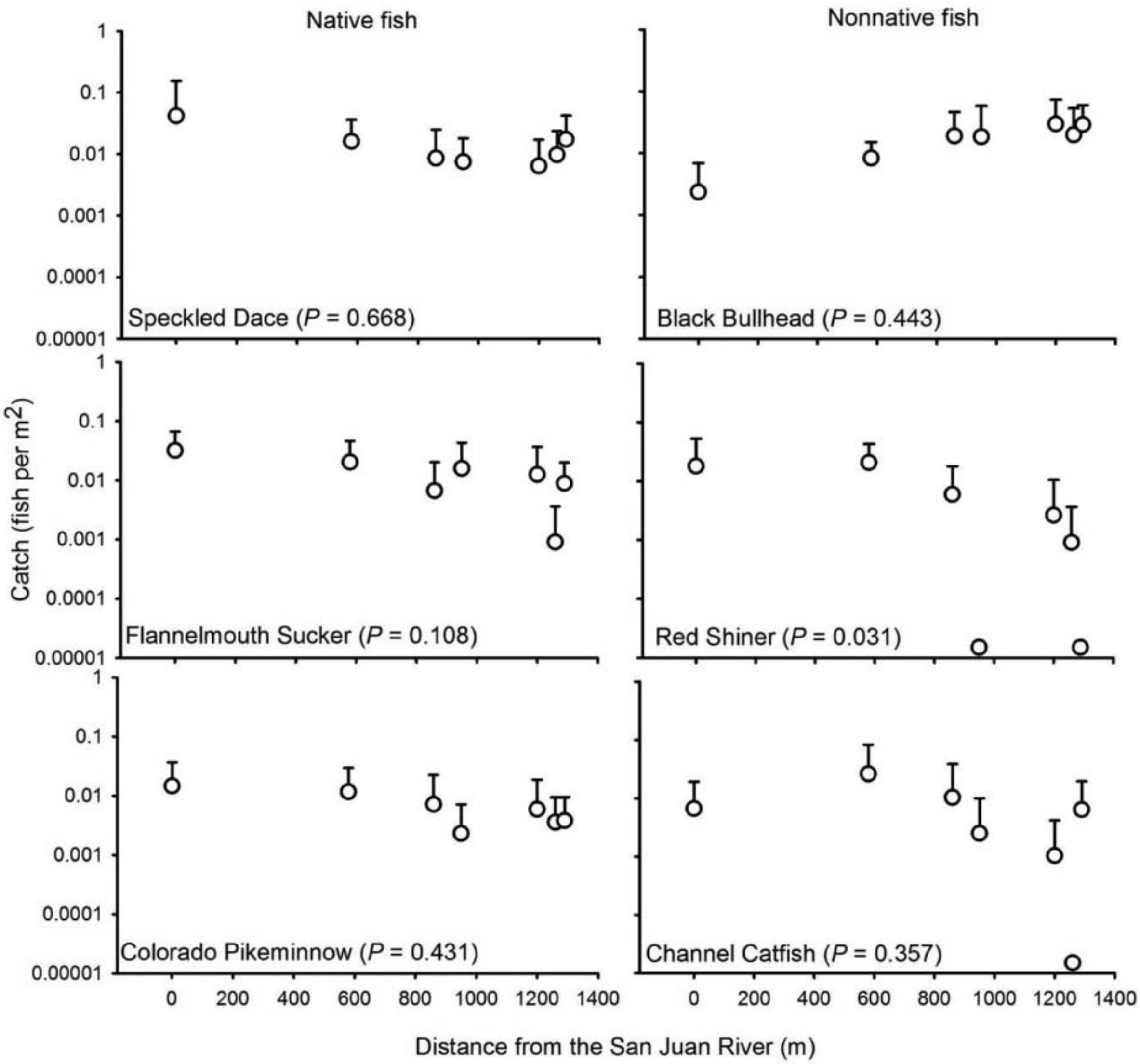

FIGURE 6. Catches of six frequently encountered species sampled from seven sites in Chaco Wash upstream from the confluence with the San Juan River during 2012 (June, July, August, and October), 2013 (March, June, August, and November), and 2014 (March). The error bars = 95% CIs; the *P*-values indicate the probabilities of the catches of the observed species differing by chance and were tested at the 0.05 level of significance.

nonnative species catches in either system. Nonnative Channel Catfish in McElmo Creek were more likely to be found throughout the stream in fall, perhaps a response to higher flows during the monsoon season. Throughout McElmo Creek, the co-occurrence of native and nonnative fishes during various times of the year could lead to negative (competitive or predatory) interactions, but such interactions may be more probable and happen more frequently at the confluence with the San Juan River (Brandenburg and Gido 1999; Gido and Propst 1999; Ryden and Smith 2002).

PIT antenna data from the Chaco Wash confluence zone, which is a stable, backwater-like habitat, indicated frequent use by several species, primarily endangered fishes. While this is partly an artifact of our sampling design (i.e., fewer nonendangered fish were tagged in upstream San Juan River habitats and Chaco Wash than in and around McElmo Creek) and was limited to one season, the data show a high frequency of use of this habitat, suggesting that it offers foraging habitat, a thermal refuge, and respite from the higher velocity of the San Juan River (Fresques et al. 2013). Backwater habitats are rare in the San Juan River (Bliesner et al. 2009), and Chaco Wash may represent a unique habitat that can constantly support fish use.

PIT tag detections at McElmo Creek supported our hypothesis that movement patterns would differ according to species. Fish movements at McElmo Creek corresponded to environmental cues related to spawning (i.e., hydrograph dynamics and temperature requirements), predictable weather activity (the monsoon season), and flow regime. Razorback Sucker

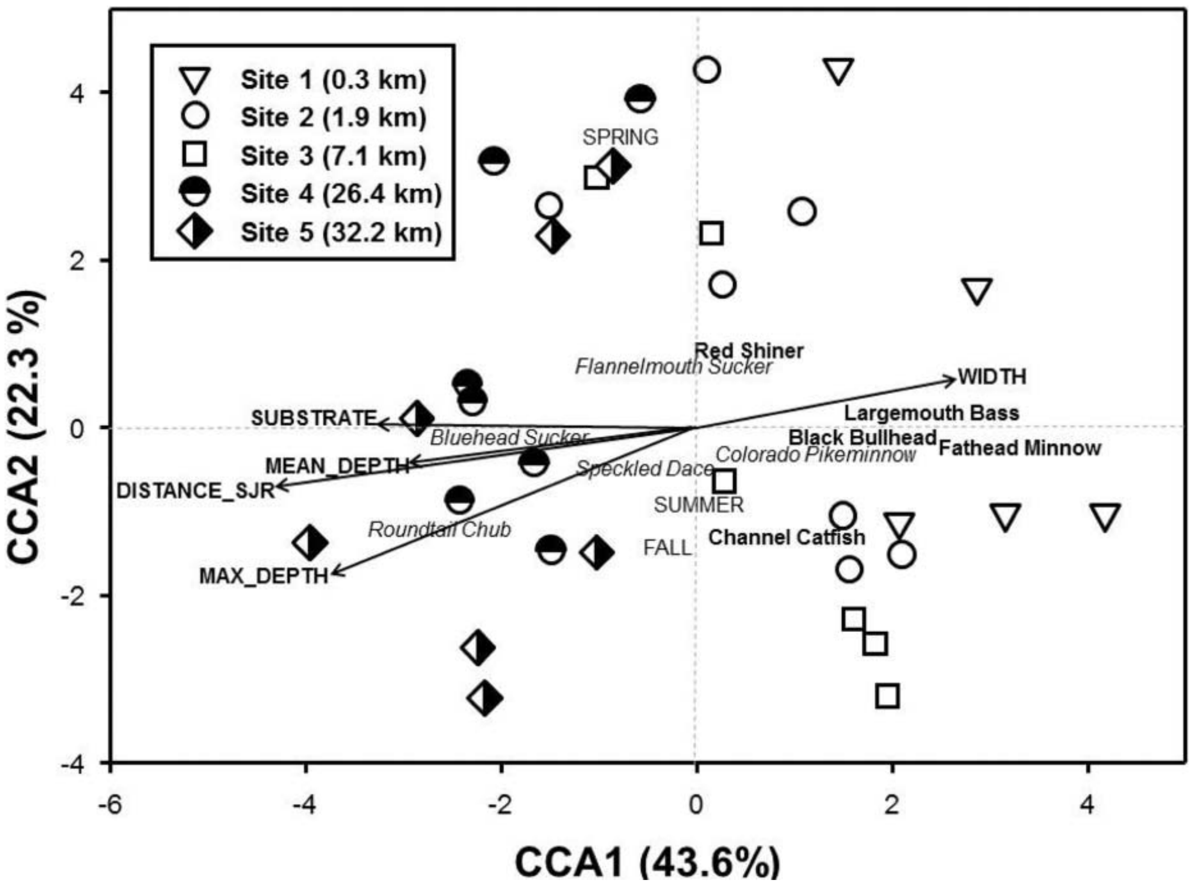

FIGURE 7. Canonical correspondence analysis (CCA) characterizing the associations of fish community structure with the environmental variables shown in Figure 2 across the sites sampled in McElmo Creek at the dates specified in that figure. The centroids for the seasonal factors (spring, summer, and fall) are shown for reference. The names of native fishes are in italics, those of nonnative fishes in bold.

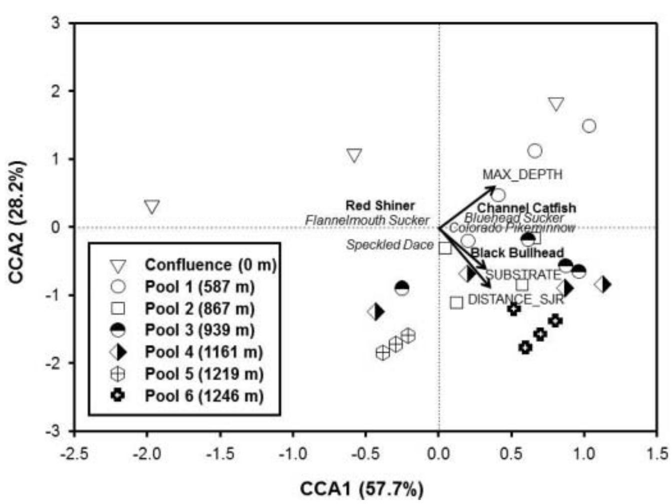

FIGURE 8. Canonical correspondence analysis of fish species constrained by site and stream morphometry across the sites sampled seasonally in Chaco Wash in June and October 2012 and March and June 2013. The names of native fishes are in italics, those of nonnative fishes in bold.

detections peaked during the late spring (especially May and June), when the ascending limb of the San Juan River hydrograph coincided with the descending or flattened limb of the McElmo Creek hydrograph. Colorado Pikeminnows were consistently detected at McElmo Creek throughout the year but appeared to be present more frequently in late fall and winter, which is associated with seasonal downstream migrations within the main stem, potentially to seek more suitable overwintering habitat with warmer water and more desirable flow regimes (Fresques et al. 2013; Durst and Franssen 2014). Flannelmouth Sucker detections showed that the most dramatic movement was associated with spawning during spring, when fish from the San Juan River moved upstream into McElmo Creek. These detections were coincident with March sampling in 2013 and 2014, which collected ripe, tuberculated males and gravid, expressing females in large aggregations throughout the creek. We find it interesting that one large-bodied species from the San Juan River, the Flannelmouth Sucker, uses McElmo Creek to spawn in massive numbers, yet similarly large-bodied Razorback Suckers have not adopted the tributary-spawning trait, suggesting they are an obligatory main-stem species. Channel Catfish in stream networks appear to have multiple movement

TABLE 3. Number of fish tagged in San Juan River, McElmo Creek, and Chaco Wash habitats between June 2012 and July 31, 2014, and detected at the latter two sites, by species. Asterisks indicate species that are not native to the San Juan River.

Species	Number tagged	Recovery site	
		McElmo Creek	Chaco Wash
Flannelmouth Sucker	3,618	1,745	7
*Channel Catfish	1,160	371	3
Razorback Sucker	1	204	86
Bluehead Sucker	300	8	0
Roundtail Chub	149	3	0
*Black Bullhead	124	15	3
Colorado Pikeminnow	77	114	34
*Common Carp	25	0	2
*Green Sunfish	20	0	0
*Largemouth Bass	8	3	0
Native hybrid sucker[a]	3	2	0
*Bluegill	1	1	0
Total	5,486	2,466	135

[a]Flannelmouth Sucker × Bluehead Sucker.

strategies, depending on season and motivation (Dames et al. 1989; Newcomb 1989; Wendel and Kelsch 1999).

The distributions of Roundtail Chub and Bluehead Suckers were restricted to upstream habitats in the McElmo Creek tributary network. This corroborates the paucity of detections at the antenna station near the mouth of McElmo Creek. The lack of Bluehead Sucker detections at the mouth of McElmo Creek can be partially explained by their abundance in the San Juan River, which is highest in upstream reaches (Franssen and Durst 2013). The very low detections of Roundtail Chub at this PIT antenna station might be explained by several factors, including historical alterations (i.e., the closure of Navajo Dam and native fish poisoning in 1962) and habitat loss in the San Juan River network, but it also is probably attributable to upstream stocking in McElmo and Yellow Jacket creeks in Colorado (Miller and Rees 2000). The upstream-oriented habitat use of Bluehead Suckers and Roundtail Chub in McElmo Creek is indicative of habitat preference, including deep pools at the most upstream site (Bower et al. 2008).

Although Colorado Pikeminnows do indeed use the McElmo Creek and Chaco Wash stream networks, more substantial investigation is needed into the potential benefits these stocked fish gain by using tributary systems (Durst and Franssen 2014). Accordingly, conservation strategies should consider using these habitats only if they enhance the probability of achieving conservation goals (i.e., promote recruitment to adulthood). Similarly, while Razorback Suckers were never encountered in upstream tributary habitats, PIT antenna detections suggest that tributary mouths offer frequently used yet relatively rare riverscape features with an unknown impact on fitness.

Including tributaries in management planning might aid in the conservation of endangered and native fishes throughout different habitats and seasons (Webber and Beers 2014). Besides showing the utility of PIT antennas in monitoring fish, our results highlight the potential for including San Juan River tributaries in efforts to remove Channel Catfish, which are potentially having a competitive and predatory influence on native fishes (Franssen et al. 2014). Predictable, seasonal movements, such as those observed in our study, provide a reasonable basis for including tributary habitats in targeted removal efforts involving weirs, electrofishing, or other means. Removal efforts in tributaries would expand on main-channel efforts, which may miss fish seeking refuge in these laterally connected systems (Franssen et al. 2014).

This study highlights an alternative to longstanding perspectives toward water development in the American Southwest. Dams and diversions are often associated with deleterious effects on native fishes by serving as sources for nonnative species, fragmenting habitats, and altering natural thermal and flow regimes (Clarkson and Childs 2000; Compton et al. 2008). However, in the systems we studied, water development created habitats that now support several native and nonnative species. McElmo Creek flows increased because of the 1986 construction of McPhee Reservoir in the Dolores River basin, which allowed for water to be transported across watersheds and ultimately led to McElmo Creek's receiving more perennial flow (Fresques et al. 2013). Chaco Wash also became more perennial after the 1961 construction of an off-channel reservoir to cool the generators of the coal-powered Four Corners Power Plant. We do not advocate further development but simply acknowledge that some systems supporting native fish communities probably would be very different and less productive without the regional water development. Due to water depletion and declines in native fishes in other small tributaries within the San Juan River basin (e.g.,

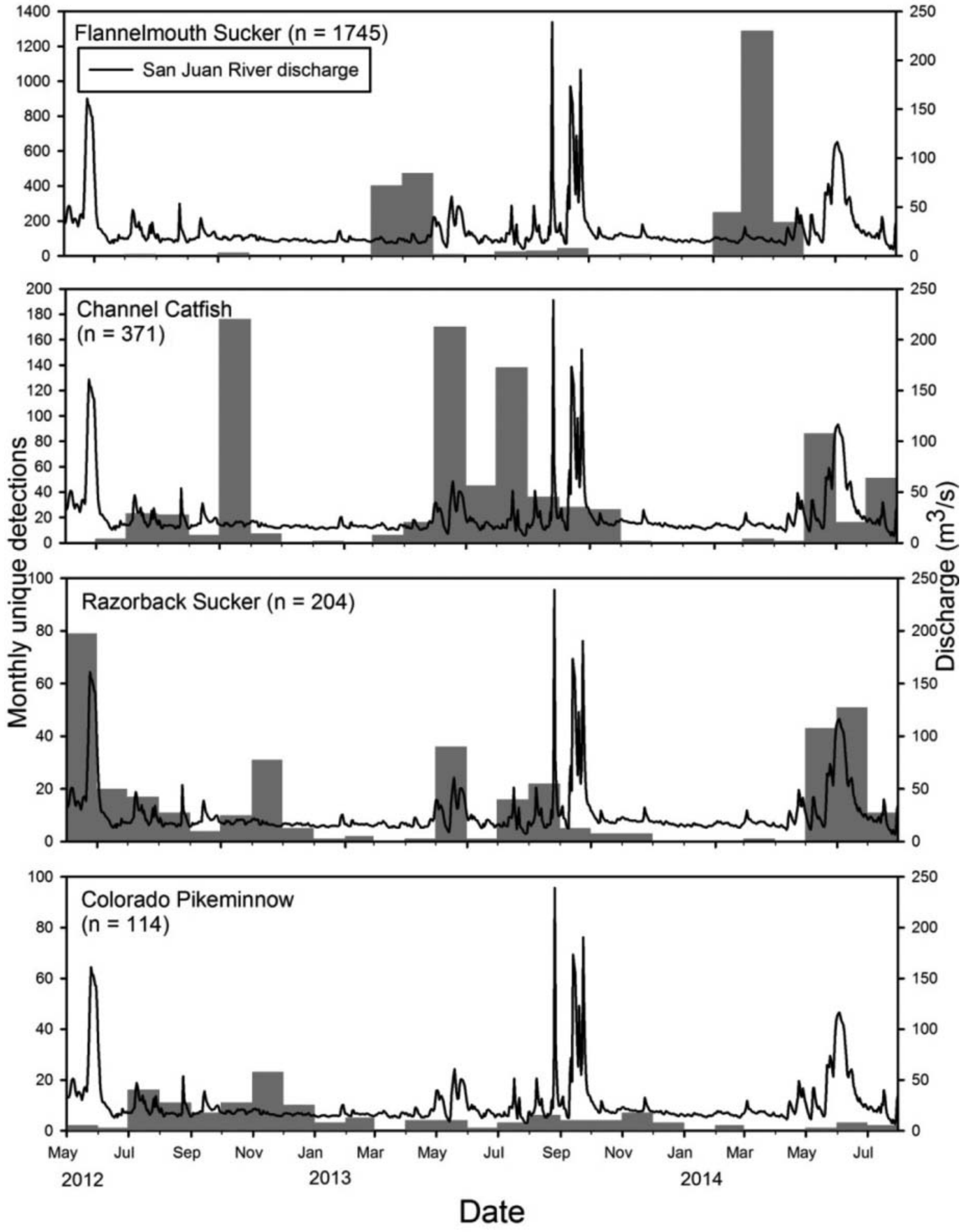

FIGURE 9. Unique monthly detections of PIT-tagged Flannelmouth Suckers, Channel Catfish, Razorback Suckers, and Colorado Pikeminnows at a PIT antenna array in McElmo Creek 150 m upstream from the confluence with the San Juan River between May 2, 2012, and July 31, 2014. Mean daily discharge for the San Juan River (USGS gauge 9379500) is shown for reference.

La Plata River and the Mancos River), McElmo Creek may harbor one (if not the only) historically similar and functional native fish community perennially connected to critical habitat in the San Juan River (Miller and Rees 2000).

Tributary networks within the Colorado River basin offer habitats suitable for increasingly broad fish community studies, if not inclusion into critical habitat designations. The San Juan River has few perennial tributaries adjacent to the middle reaches of the main stem, so the ones that do exist offer unique habitat in this river network. Conservation of fishes and aquatic environments in arid regions can benefit from studies that include community distributions and movements among perennial and ephemeral systems, especially those that have been extensively modified in the past and that are expected to change in the future.

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